Evolution trends in Middle Carboniferous Petalaxidae (Rugosa)

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ABSTRACT
Various aspects of the study of the Petalaxidae Fomichev, 1953 are considered. Detailed observations from previous investigations together with new, more precise data on the stratigraphic distribution of the Petalaxidae in the northern and central part of the Russian Platform are used as a framework for phylogenetic reconstruction. Five main morphological groups are recognized within *Petalaxis* Milne Edwards *et* Haime, 1852, based on the combination of stable and variable features predominant in each group. The main trend in Petalaxidae evolution during the Bashkirian and Moscovian stages is an increase in the colony integration and the stabilization of multitrabecular septal structure. The diagnosis and species content are given for taxa included in Petalaxidae after author's revision. Four new taxa are described: *Donastraea* n.g., *Ivanovia (Procystophora)* n.sg., *Petalaxis (Petelaxis) primitivum* n.sp. and *P. (P.) gigas* n.sp.

KEY WORDS
Peri-Tethys,
Petalaxidae,
Middle Carboniferous,
phylogeny,
biostratigraphy,
microstructure,
new taxa.

RÉSUMÉ

Tendances évolutives des Petalaxidae (Rugosa) du Carbonifère moyen. Des aspects variés de l'étude des Petalaxidae Fomichev, 1953, sont considérés dans cette publication. Des observations détaillées provenant d'investigations anciennes et récentes, des données plus précises sur la distribution stratigraphique des Petalaxidae dans la partie septentrionale et centrale de la plate-forme russe sont utilisées comme un guide pour la reconstruction phylogénétique. Cinq groupes morphologiques principaux sont reconnus dans *Petalaxis* Milne Edwards *et* Haime, 1852, fondés sur la combinaison de caractères stables et variables prédominant dans chaque groupe. La principale tendance évolutive des Petalaxidae pendant le Bashkirien et le Moscovien est une croissance dans l'intégration coloniale et la stabilisation de la structure septale multitrabéculée. La diagnose et le nombre d'espèces sont donnés par taxons inclus dans les Petalaxidae, d'après la révision de l'auteur. Quatre nouveaux taxons sont décrits : *Donastraea* n.g., *Ivanovia (Procystophora)* n.sg., *Petalaxis (Petalaxis) primitivum* n.sp. and *P. (P.) gigas* n.sp.

MOTS CLÉS
Péri-Téthys, Petalaxidae (Rugosa), Carbonifère moyen, phylogénie, biostratigraphie, microstructure, nouveaux taxa.

INTRODUCTION

Based on previous data (Hill 1981; Sando 1983) the Petalaxidae range from Early Carboniferous (Visean) to Early Permian. This investigation shows that the Middle Carboniferous Petalaxidae are a remarkably widespread, abundant and short-lived taxonomic group. They range through uppermost early Bashkirian, late Bashkirian and Moscovian stages (Fig. 3), and are found in the Urals, Arctic Canada, U.S.A., Northern Timan, Novaya Zemlya, Moscow and Donetz Basins, China, Japan, Thailand, Cantabrian Mountains, Alaska and North Africa. Thus, they occur in the shelf facies in the Tethyan and the North American-Uralian basins. They are also known in Spitsbergen and Arctic Canada (Bamber & Fedorowski 1995; Somerville 1997).

MATERIAL

The data for this study were obtained from bed to bed collections of coral faunas from the uppermost Early Bashkirian-Moscovian of the Novaya Zemlya Archipelago (Cape Makarov, Northern Island), Sula River and Malaya Pokayama sections of Northern Timan (Figs 1, 2) and some sections of the Moscow region. Also, new material collected from the Moscow Basin was included and the works of Dobrolyubova (1935) and Fomichev (1953) were revised.

STRATIGRAPHIC POSITION

Two partial-range zones, the *Petalaxis* zone and the *Ivanovia* zone, have been defined (Kossovaya 1995), based on the evolutionary patterns shown by the Petalaxidae from the uppermost Early Bashkirian to the top of the Moscovian stage. The determination of the partial-range generic zone boundaries was based on taxonomic diversity dynamics, the structure of the assemblages and phylogeny of the Petalaxidae. Analysis and estimation of zonal boundaries show that the more precise levels for correlation are those characterized by the biotic events in the development of the coral assemblages (extinction, initial phase of recovery and radiation). Three main phases of variation in rugosan diversity were distinguished after the abrupt elimination of many genera as a result of the Mid-Carboniferous event (base of *Homoceras* zone, Kossovaya 1996, fig. 3). These data have been used for international correlation (Kossovaya 1996, fig. 8), but now should be modified a little.

THE *Petalaxis* ZONE

The appearance of Bashkirian representatives of *Petalaxis* coincides with the stabilization of favourable marine conditions and marks the beginning of the recovery interval that correspond to the base of the *Petalaxis* zone. It begins approximately at the base of the *praegorskyi-staffelliformis* fusulinacean zone (= *Streptognathodus expansus-Idiognathodus sinuosus* conodont zone (Koren 1989)) with the sudden appearance and rapid expansion of massive colonial *Petalaxis* along the eastern margin of the Euro-american paleocontinent (Fig. 5). This boundary was observed in Novaya Zemlya and Northern Timan sections and has been documented in the Bashkirian Mountains stratotype region (Ogar 1985). This level is also emphasized by diversification of solitary and fasciculate corals (Kossovaya 1996). In the Cape Makarov section (Novaya Zemlya, Loc. 801, Fig. 1) the first representatives of *Petalaxis primitivum* n.sp. (*P. stylaxis* group) were found with *Pseudostaffella antiqua*, *P. grandis* and *P.* cf. *praegorskyi* (determined by Dr. V. Davydov, Fig. 1). In the Sula River section (northern Timan), at Loc. 31 (bed 9) *Petalaxis*, represented by *P. persubtilis* Kozyreva, 1974 which occurs together with *Donophyllum reticulatum* (Fomichev, 1953) (bed 9) and *Yakovleviella tschernysnhewi* (Gorsky, 1978). The first occurrence of *P.* sp. aff. *P. mcoyanus* Milne-Edwards *et* Haime, 1851 was fixed in the Askynbashskian substage in the Southern Urals (Ogar 1985). Numerous species of *Petalaxis* are known from the Bashkirian deposits of the Voronezh uplift. The Early Bashkirian interval is characterized by *P. persubtilis* Kozyreva, 1974, *P. korkhovae* Kozyreva, 1974, *P. immanis* Kozyreva, 1974, *P. exilis* Kozyreva, 1974 and *P. confertus* Kozyreva, 1974 (Fig. 5). Some of these species extend into the Late Bashkirian, where *P. mirus* Kozyreva, 1974, *P. evidens* Kozyreva, 1974 also appear (Kozyreva 1974, 1984). In the Cantabrian Mountains *Petalaxis* occurs in the equivalent Westphalian A (Rodriguez 1984; Rodriguez *et al.* 1986). In Arctic Alaska (Northern Flank, Eastern Brooks Range) *Petalaxis wahooensis* is found at the base of the Atokan stage (foraminiferal zone 21, Armstrong 1972). *Petalaxis* was shown in the list of Bashkirian genera in the midcontinent and the western interior of USA by Sando (Rodriguez *et al.* 1986; Sando 1989). The precise stratigraphic position of *Petalaxis* is known from four southern Midcontinent Morrowan localities, all associated with the *Idiognathodus sinuosus* conodont zone (Sutherland & Grayson 1992).

The appearance of *Petalaxis* [*P. kitakamiensis* (Minato, 1955)] was fixed in grainstone or packstone beds of Bashkirian age near Ban Tat So (Km 13), Thailand (Fontaine *et al.* 1991). The level of the *Petalaxis* appearance seems to be useful for international correlation and allows to correlate the base of *Petalaxis* zone with the middle part of Morrowan and the base of the Westphalian A (see Kossovaya 1996, fig. 8).

After the decrease of diversity until Vereian substage (Fig. 3) in which no new species appeared, *Petalaxis* reached its greatest geographic distribution in the Kashirian substage. Some species with internal structure differing from those in the Bashkirian appear in the Kashirian of the eastern part of Russian Platform (Oka-Zna uplift, Studentz quarry). The predominance of massive colonial *Petalaxis* defines the *P. mcoyanus* zone in the Donets Basin (Zonal Stratigraphy 1989). *P. stylaxis uralica* (Gorsky, 1978) occurs in coeval deposits of Gornaya Bashkiria, in the Urals (Ogar 1990). The number of species is not very high, only the main branch still exists (Fig. 5). In different regions, coral diversity begins to increase: in interval 12 of the western interior of USA, at the beginning of the Westphalian C, in the base of the Kashirian substage in the Moscow region (post-Vereian increase of diversity in recovery interval, Kossovaya 1996)

THE *Ivanovia* ZONE

The appearance of astreoid colonies within one of the *Petalaxis* branch seems to be the most remarkable event in the family evolution. The first representatives of *Ivanovia* Dobrolyubova, 1935 appear in the Podolsk quarry (stratotype of the Podolskian substage, Moscow region, Kossovaya's collection) and then become abundant in the Myachkovian substage, where the *Petalaxis vesiculosus* (Dobrolyubova, 1935) group is dominant (Fig. 6). *Ivanovia podolskiensis* Dobrolyubova, 1935 is known from the Uppermost Kashirian and Podolskian substages in the Cantabrian Mountains, Asturias, Spain (Escalada Formation) (Rodriguez 1984). The first appearance of *Ivanovia* coincides approximately with the base of

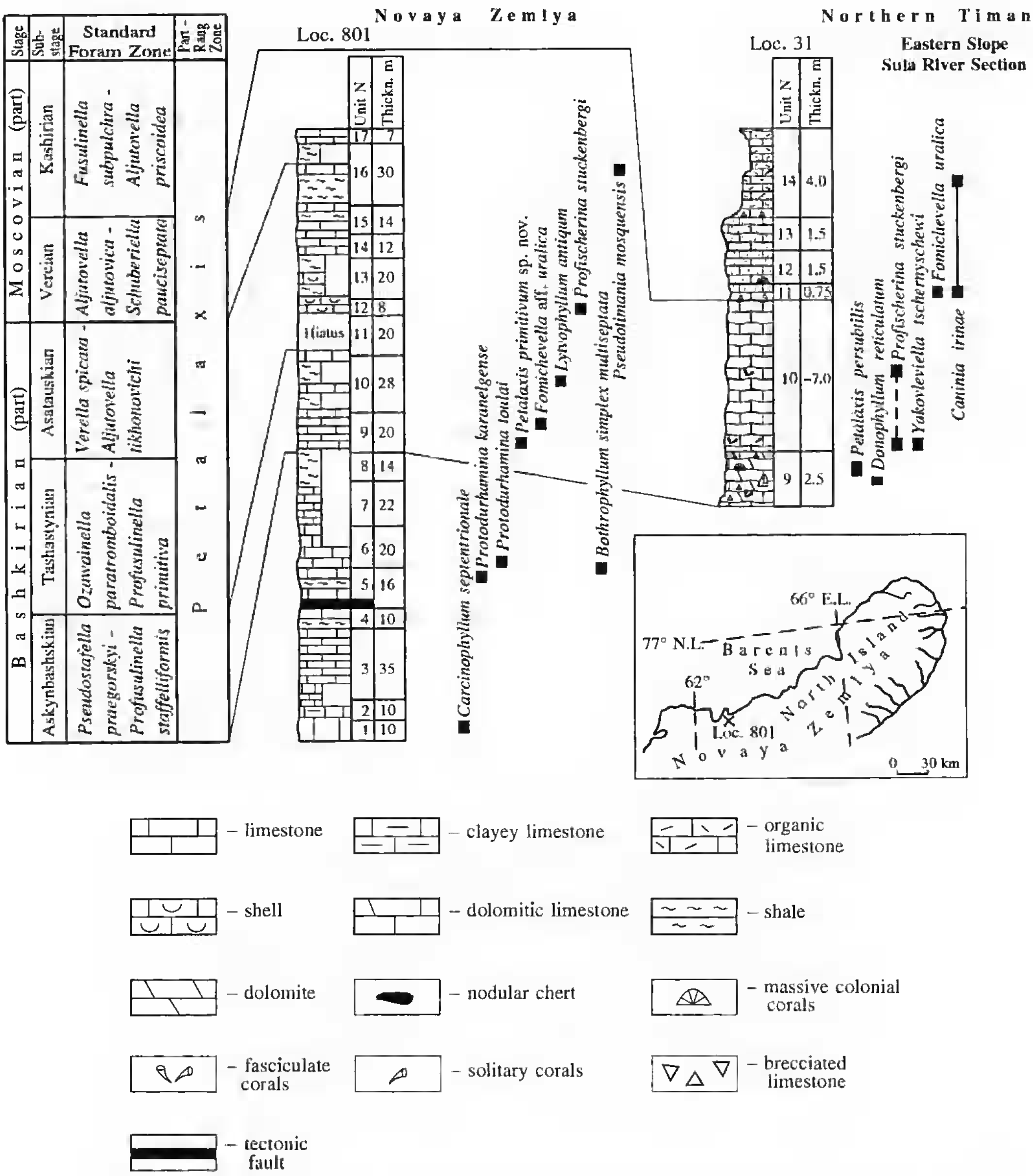

FIG. 1. — The occurrence of *Petalaxis* and associated species in the Bashkirian and Early Moscovian deposits of the northern part of Russia (loc. 801, northern island of Novaya Zemlya; loc. 31, Northern Timan, Sula River section).

the Podolskian substage (Figs 3, 5, 6), which is considered to be the beginning of the radiation of the Petalaxidae and is defined as the lower boundary of the *Ivanovia* zone (the base of *colaniae-vozhgalensis-kamensis* foraminifera zone, Fig. 5). In the Donets Basin, *Ivanovia* occurs from limestones K8-L6 (Fomichev 1953), slightly below the first appearance of *Ivanovia* in the type area. The maximum diversity of *Petalaxis* and astreoid forms is record-ed in the Myachkovian substage, especially in the Donets and Moscow Basins, where numerous species of *Ivanovia* (*Ivanovia*) (Dobrolyubova, 1935), *I.* (*Procystophora*) n.sg., *Donastraea* n.g. and *Cystophorastraea* Dobrolyubova, 1935 (Fig. 15) occur. In the radiation interval (Figs 5, 6) all groups of *Petalaxis* exist almost simultaneously,

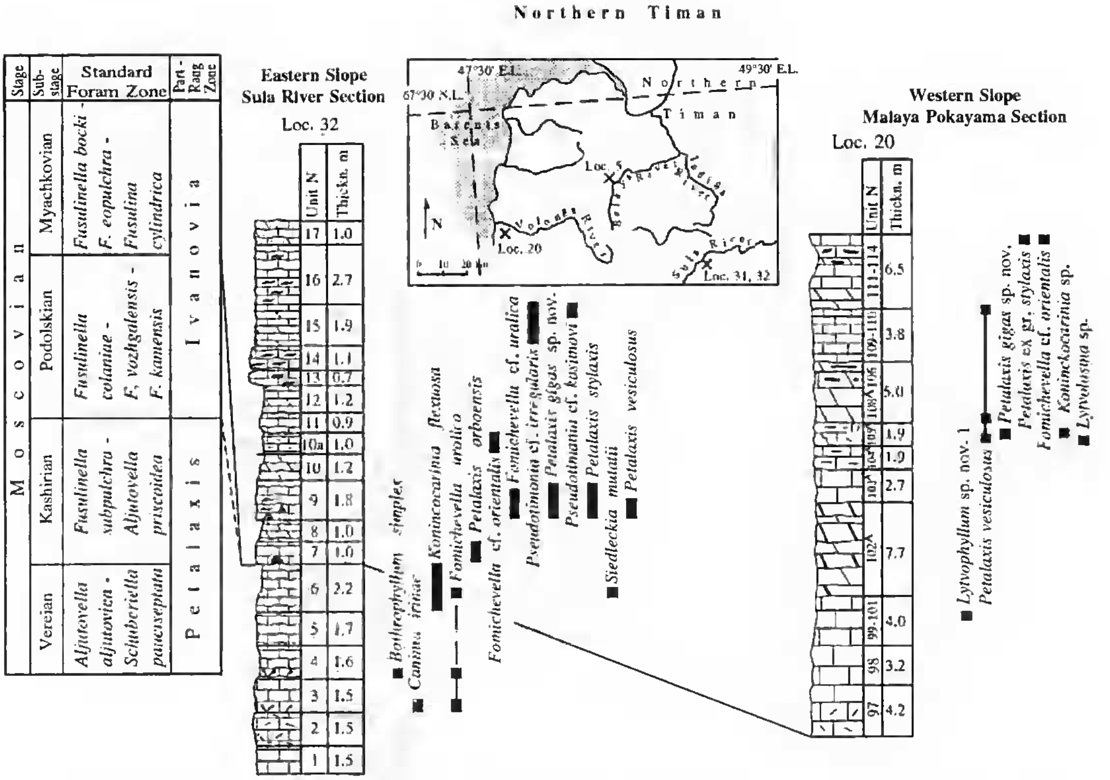

FIG. 2. — The occurence of *Petalaxis* and associated species in the Moscovian deposits of the northern Timan sections (see legend Fig. 1).

but the *P. vesiculosus* group is most widespread. This interval is defined as the *Petalaxis vesiculosus* species-range zone in the northern Timan sections (Kossovaya 1995) and is also characterized by *P. flexuosus* (Trautschold, 1879) (Moscow Basin, northern Timan, Belaya River section), *P. gigas* Kossovaya n.sp. (Northern Timan, Sula River section and Malaya Pokayama section), *P. orboensis* (de Groot, 1963) and *P. stylaxis* (Trautschold, 1879) (Moscow Basin). In the Malaya Pokayama section *P. gigas* n.sp. (*vesiculosus* group) was found together with index-species of the *Neognathodus roundyi-Streptognathodus cancellosus* conodont zone (zonation by Goreva *in* Goreva & Kossovaya 1997). In Belaya River section, *P. flexuosus* (loc. 5, bed 5-7) was found in the limestone, overlying that containing the *Parastaffella bradyi* Moeller, 1877 and *Parastaffella moelleri* Ozawa, 1925 (determined by Alekseeva, pers. com.). These foram species are widespread in Moscovian deposits of the Russian Platform. In the type section of the Myachkovian substage at Domodedovo quarry, *Petalaxis* species (*stylaxis*, *flexuosus*) occur in the lower part of substage (Novlinskaya Formation) and the last representatives of *P. stylaxis* group occur in the upper part of Sula Formation in the Malaya Pokayama section (bed 113) slightly below the Moscovian/Kasimovian boundary (Fig. 2). In most areas of western Russia, the Petalaxidae became extinct before the end of the Myachkovian.

Ivanovia zone coincides with radiation phase, which is easily recognisable in Novaya Zemlya, in the Moscow Basin and surrounding area and in the Northern Timan section at the base of the *colaniae-vozhgalensis-kamensis* zone (Fig. 5) at the base of Podolskian substage on the Russian Platform. In addition, the peak of diversity is fixed in the base of Westphalian D, and the base of the Desmoinesian (Interval 13, Western interior, USA, Sando 1989). *P. yosti* Stevens, 1995 (belonging to *P. Grootia* group) occured in Bird Spring Formation of the Desmoinesian (Stevens 1995) and could be correlated with the upper part of Moscovian.

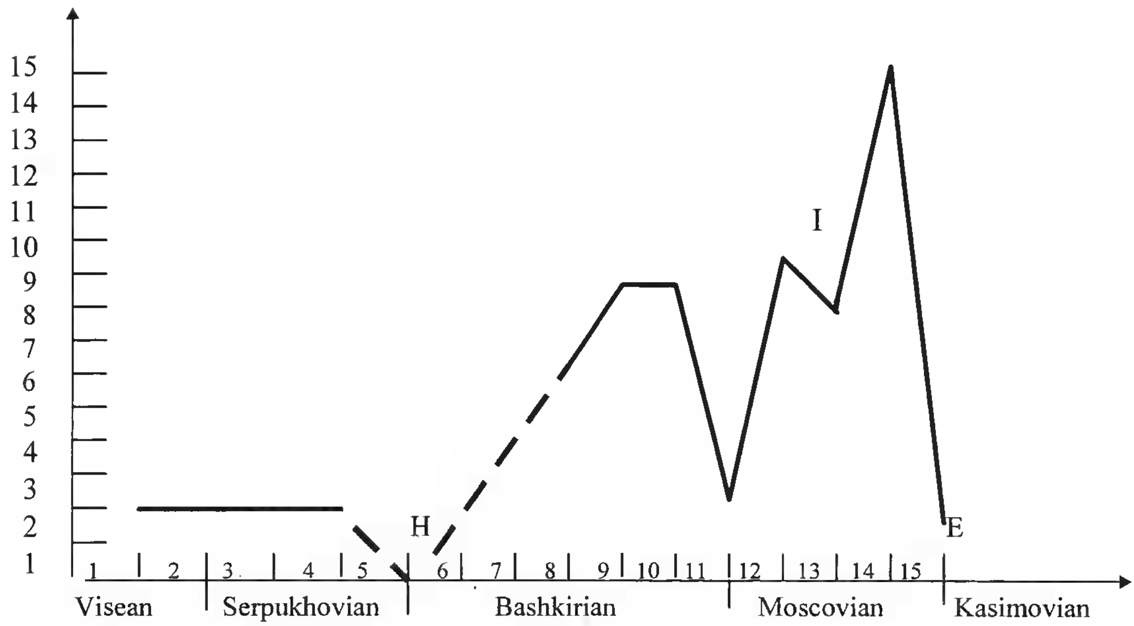

FIG.3. Taxonomic diversity of Petalaxidae Fomichev, 1953. **I**, innovation level at the base of Podolskian substage; **H**, hiatus in the Petalaxidae distribution at the end of Serpukhovian and the beginning of the Bashkirian; **E**, extinction at the end of the Moscovian. **1-15**, foram zones of the Russian Platform (Zonal Stratigraphy 1989). **Visean**: **1**, *Eostaffella ikensis*; **2**, *Eostaffella tenebrosa*, *Endothyranopsis parvus*. **Serpukhovian**: **3**, Tarusian-Steshevian substages, *Pseudoendothyra globosa*, *Neoarchediscus parvus* zone; **4**, Protvian substage, *Eostaffella protvae* zone; **5**, Zapaltubian substage, *Eosigmolina explicata*, *Monotaxinoides subplana* zone. **Bashkirian**: **6**, Voznesenskian substage, *Plectostaffella bogdanovskensis* zone; **7**, Syranian substage, *Eostaffella pseudotruvei*, *E. postmosquensis*, *E. varvariensis* zone; **8**, Akavasskian substage, *Pseudostaffella antiqua*; **9**, Askynbashian substage, *Pseudostaffella praegorsky*, *Profusulinella staffelliformis*; **10**, Tashastynian substage, *Ozawainella pararhomboidalis*, *Profusulinella primitiva*; **11**, Asatauskian substage, *Verella spicata*, *Aljutovella tikhonovichi*. **Moscovian**: **12**, Vereian substage, *Aljutovella aljutovica*, *Schubertella pauciseptata*; **13**, Kashirian substage, *Fusulina pseudoelegans*, *Aljutovella znensis*; **14**, Podolskian substage, *Fusulinella colaniaea*, *F. vozhgalensis*, *Fusulina kamensis*; **15**, Myachkovian substage, *Fusulinella bocki*, *F. eopulchra*, *F. cylindrica*. **Kasimovian**: Krevyakinian substage, *Protriticites pseudomontiparus*, *Obsoletes obsoletus*.

TAXONOMIC REVIEW

The Family Petalaxidae was established by Fomichev (1953) (Fig. 4). According to his initial diagnosis, only genera of massive colonial corals with a continuous intercorallite wall, a lamellar, complex axial structures containing axial dissepiments and/or axial plates were included in this family. The dissepimentarium consists of large dissepiments interrupting the septa. Within this family, Fomichev (1953) recognized only one genus *Petalaxis* Milne Edwards *et* Haime, 1852 (type species *P. mcoyanus* Milne Edwards *et* Haime, 1852) including the subgenus *Cystolonsdaleia* Fomichev, 1953. According to Fomichev (1953), a possible ancestor could be *Thysanophyllum* Nicholson *et* Thomson, 1876 or *Endophyllum* Milne-Edwards *et* Haime, 1851 (Early Carboniferous). Similar corals, distinguished by an interrupted intercorallite wall, were grouped into the Family Cystophoridae Fomichev, 1953. It embraced *Ivanovia* Dobrolyubova, 1935, *Cystophora* Yabe *et* Hayasaka, 1916, *Polythecalis* Yabe *et* Hayasaka, 1916, and *Lonsdaleiastraea* Gerth, 1921 with the possible ancestor *Thysanophyllum*. Later Hill (1981) revised Fomichev's systematics and included all of these genera, partly as junior synonyms, into one family (the Petalaxidae), and changed the family diagnosis accordingly. Sando

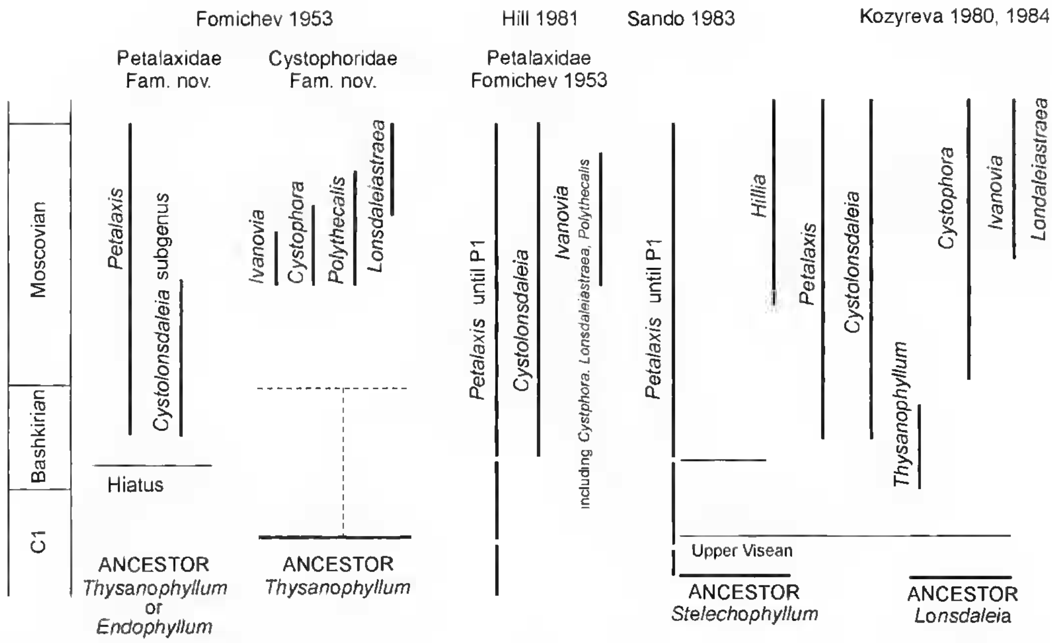

FIG. 4. — Historical review of previous investigations showing stratigraphic range of genera within Petalaxidae. Hiatus in the Petalaxidae distribution embraces Voznesenskian, Syranian and Akavasskian substages (Bashkirian stage). **C1**, Early Carboniferous.

(1983) published a very important revision of *Petalaxis*, where five species groups were distinguished: the *simplex* group, the *flexuosus* group, the *wagneri* group, the *mcoyanus* group, and the *vesiculosus* group. *Stelechophyllum* Tolmachev, 1933 (Lithostrotionidae) was suggested as a possible ancestor. Kozyreva (1984) dealt with the evolutionary aspects of the Petalaxidae, where *Lonsdaleia* Mc Coy, 1849 was suggested as a possible ancestor. The present investigation and supporting phylogenetic reconstruction makes some changes to Hill's (1981) system, but follows a few of the main principles established (Hill 1938; Sando 1983) in general aspect, but in a somewhat modified form:

– comparison of the adult stages of different species;
– investigation of variability within one species;
– use of budding and early stages of development for recognition of the connection between species (genera) based on the recapitulation law;
– comparative analysis of septal microstructure;
– use of different type of stratigraphic data, including event stratigraphy as a framework for a phylogenetic model.

TAXONOMIC DIVERSITY ANALYSIS

The first appearance of species included in *Petalaxis* is suggested from the Late Visean deposits of North America [*P. simplex* (Hayasaka, 1936), Little Flat Formation, Utah] (Bamber 1961; Sando 1983). *P. simplex* is characterized by very short major septa, which are poorly expressed in the early stages of corallite development (Sando 1983, plate 18, fig. 1). The taxonomic diversity analysis of the Petalaxidae shows an interruption of *Petalaxis* lineage and associated genera in the uppermost Serpukhovian-lowermost Bashkirian (Fig. 3). Disappearance at that level affects not only *Petalaxis* species, but numerous taxa of rugose corals and has been described as a minor mass extinction event (Kossovaya

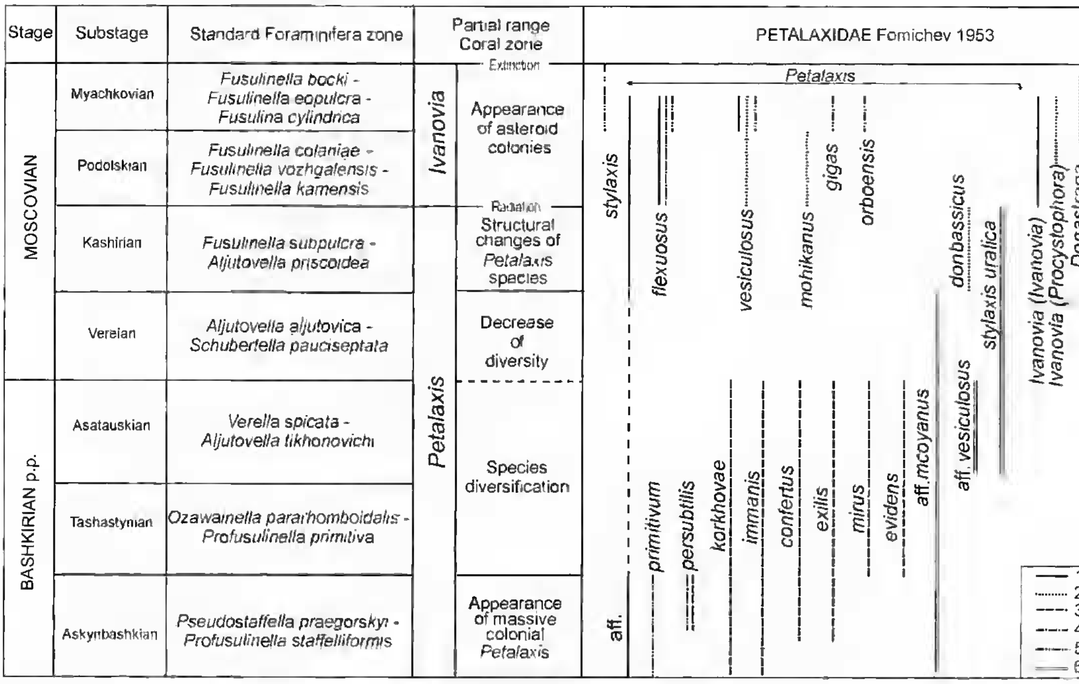

FIG. 5. — Distribution and stratigraphic range of *Petalaxis* and *Ivanovia* species in the Bashkirian and Moscovian deposits of the western part of Russia. **1**, Moscow Basin; **2**, Donets Basin; **3**, Voronezh anticline; **4**, Nova Zemlya; **5**, Northern Timan; **6**, Gornaya Bashkiria. N.B. Early Bashkirian substages omitted (see Fig. 6).

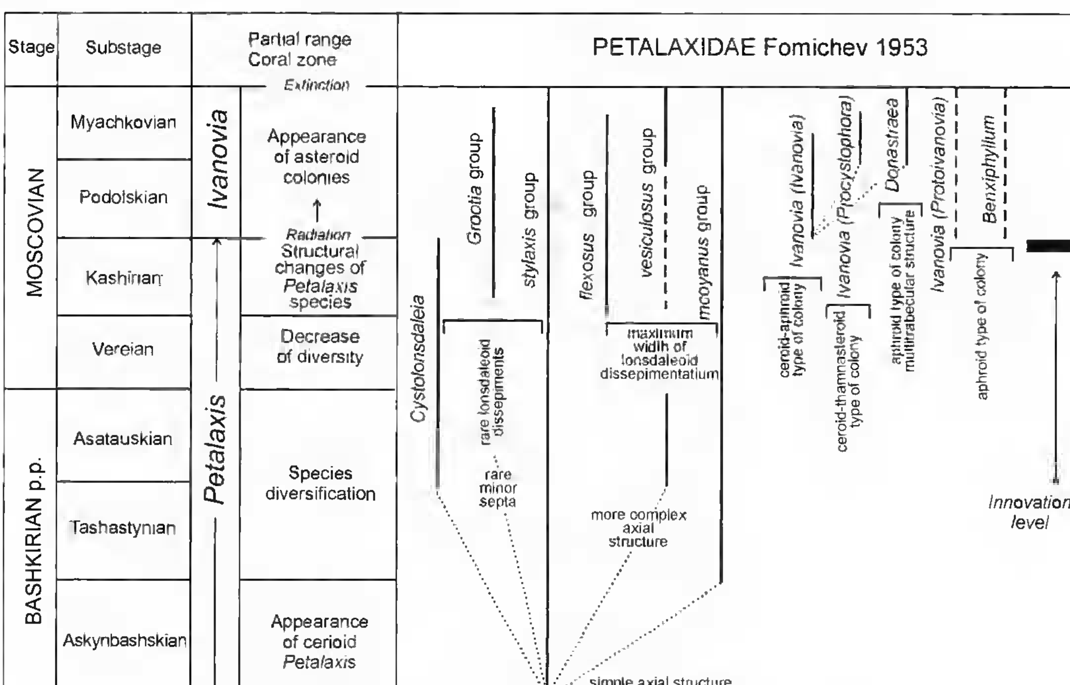

FIG. 6. — Phylogenetic relations between morphogenetic groups within Petalaxidae.

1996). The distribution of the Petalaxidae is restricted by extinction of the most species before the begining of the Kasimovian. Permian representatives of *Petalaxis*, numerous in the Wolfcampian deposits of California (Wilson 1982) are absent from the Kossovaya's collection and everywhere in Russia, and are not considered here. The punctuated character of diversification of the Petalaxidae is expressed by two remarkable hiatuses: one near the mid-Carboniferous boundary and another near the lower Kasimovian boundary (Figs 3, 5). During the uninterrupted sequence within the Bashkirian and Moscovian, a significant decrease in the diversity occurs at the base of the Vereian substage (Fig. 5) coinciding with stabilization of conditions unfavourable for massive corals. The beginning of a short transgression followed by the abrupt change to regression took place during the Vereian in the Moscow Basin (Briand *et al.* 1998). The same diversity pattern is characteristic for coeval deposits of the Urals (Gorsky 1978; Ogar 1984, 1990). A gradual increase in diversity is characteristic for the Kashirian substage. The appearance of *Petalaxis* at the middle of this substage in the Moscow Basin coincides with a transgressive system tract (Studenetz Quarry) (Briand *et al.* 1998). Adaptive radiation and widespread expansion of the Petalaxidae occur in the Podolskian substage and coincides with the appearance of morphological innovation, characterized by a type of colony with a higher degree of integration (aphroid and thamnasterioid colonies of *Ivanovia* and *Donastraea*). In the Moscow Basin, the levels of Petalaxidae radiation and the appearance of astreoid colonies also coincides with a maximum flooding surface (Briand *et al.* 1998). The disappearance of Petalaxidae in the Moscow Basin can be illustrated in Domodedovo quarry where it is correlated with a regression at the base of Peski Formation at the end of the Myachkovian time. Only one species (*stylaxis* group) with maximum morphological simplification has been found near the Moscovian-Kasimovian boundary and may be considered as the last species of long-living lineage of the *Petalaxis* genus.

There are some data on longer duration (Late Carboniferous) of very restricted assemblage of astreoid colonies in the Donets Basin (Fomichev 1953) and China (*I. jiaozuoensis* Peng, Lin *et* Li, 1992).

SYSTEMATICS

Family PETALAXIDAE Fomichev, 1953

Petalaxidae Fomichev, 1953: 449-452. – Hill 1981: F 401. – Sando 1983: 23-40. – Bamber & Fedorowski 1995: 4.

Cystophoridae Fomichev, 1953: 469 (type genus *Cystophora* Yabe *et* Hayasaka, 1916)

TYPE GENUS. — *Petalaxis* Milne-Edwards *et* Haime, 1852.

GENERA INCLUDED. — *Petalaxis* Milne-Edwards *et* Haime, 1852; *Petalaxis* (*Petalaxis*) Milne-Edwards *et* Haime, 1852; *P.* (*Grootia*) X. Yu, 1984; *Cystolonsdaleia* Fomichev, 1953; *Ivanovia* (*Ivanovia*) (Dobrolyubova, 1935); *I.* (*Procystophora*) n.sg.; *I.* (*Protoivanovia*) X. Yu, 1977; *Benxiphyllum* Wu *et* Lin, 1992.

AGE. — Early Carboniferous?, Middle Carboniferous, Early Permian?.

DIAGNOSIS. — Cerioid, cerioid-astreoid, aphroid and thamnasterioid; axial structure represented by lathlike columella conjoined with long cardinal septum, becoming narrow axial column by addition of few, short septal lamellae and axial tabellae. The latter forms the discontinious column wall. Periaxial tabulae subhorizontal or concave or decline abaxially. Some taxa have a very complete axial structure similar in texture to cone in cone. Tabular subhorizontal or slightly con-cave or convex. Dissepimentarium commonly lonsdaleoid. Microstructure from mono- to multitrabecular.

REMARK

The proposed phylogeny model (Fig. 6) is based on the comparative analysis of the following morphological features and estimation of their variability and stability.

Such morphological features are considered to be important: the number of rows of dissepiments, the complexity of the axial structure, the ratio of the width of dissepimentarium to diameter of tabularium, the degree of development of minor septa. This is the basis for distinguishing several main groups within the *Petalaxis* genus showing independent evolution trends of the each lineage.

Some of this group have to be considered as a subgenus after redescription of most of the species.

Discussion

By the Kossovaya's opinion, based on the observation of *Petalaxis* species in the American Museum of Natural History (Washington), the Early Carboniferous species, which had been included in the *Petalaxis* genus by Sando (1983) have to be revised from the point of microstructure. By their morphological macrofeatures, they are more similar to *Stelechophyllum* Tolmachev, 1933 (Sando 1983).

Genus *Petalaxis* Milne-Edwards *et* Haime, 1852

Petalaxis Milne-Edwards *et* Haime, 1852: 205. – Fomichev 1953: 449-452;. – Hill 1981: 401. – Sando 1983: 23-25;

Stylaxis Milne Edwards *et* Haime, 1851: 452 (part.).

Lithostrotionella Yabe *et* Hayasaka, 1916 – Dobrolyuhova 1935: 14.

Lonsdaleia Mc Coy, 1849 – Dobrolyubova 1935: 29.

Type species. — *Petalaxis mcoyana* Milne-Edwards *et* Haime, 1852. Lectotype: sample 1/251, St Petersburg State University, Museum of Historical Geology department (Fedorowski & Gorianov 1973: 58-59, pl. XII, fig. 4, text-fig. 20).

Age and locality. — Middle Carhoniferous, Moscovian stage, Myachkovian horizon, Moscow region, Myachkovo village (Fedorowski & Gorianov 1973).

Diagnosis. — Cerioid colonies; corallites with simple, narrow axial structure of lathlike columella continuous with one or two long protosepta, commonly cardinal one, reinforced by one or two very short septal lamellae and sparse, steep axial tabella next below; other major septa withdraw from axis; dissepimentarium of different width; tabulae subhorizontal; supplemented peripherally by abaxially declined tabellae. *Petalaxis* genus includes four morphogenetic groups of *Petalaxis* (*Petalaxis*): *stylaxis, flexuosus, vesiculosus, mcoyanus* and *Petalaxis* (*Grootia*).

Subgenus *Petalaxis* (*Petalaxis*) Milne-Edwards *et* Haime 1852

Diagnosis. — As for genus, excluding representatives with weak development of lonsdaleioid dissepiment.

Petalaxis (*P.*) *stylaxis* group (Figs 7, 13C, D, 15A, B, 16A, B; Table 1)

Species included. — *P.* (*P.*) *stylaxis* (Trautschold, 1879), *P.* (*P.*) *primitivum* n.sp., *P. kitakamiensis* (Minato, 1955), *P. penduelensis* (de Groot, 1963).

Age. — Late Bashkirian-Moscovian, Early Kasimovian?.

Diagnosis. — Cerioid colonies with complete intercorallite wall, simple axial structure, composing the thickened end of cardinal septum or conjoined cardinal and counter septa. Dissepimentarium from 1-3 rows of dissepiments, but constant. Minor septa are very short or inconstant. The earliest species, belonging to the *P. stylaxis* group, are characterized either by a very simple axial structure or by conjoined cardinal and counter septa. They became longer in Moscovian species. In their earliest growth stage, the corallites have no dissepiments. Only a few rows of dissepiments are characteristic for the adult stages of the Bashkirian *Petalaxis* (*P.*) *primitivum* n.sp. (Fig. 7G, H). The Myachkovian *Petalaxis* (*P.*) *stylaxis* is characterized by thicker axial structure and by variation in the length of minor septa at maturity (Fig. 7A-F). The trend from reduced minor septa, typical for Bashkirian representatives, to variable minor septa in those of the Moscovian seems to be the evolutionary trend within this group. The most stable features are: (1) the number of dissepiments rows (1-3); (2) a simple axial structure; (3) the ratio of dissepimentarium width to tabularium diameter Wdis/Drab is about 0.2-0.3 (Table 1).

Petalaxis* (*P.*) *primitivum n.sp. (Figs 7G-I, 16A, B; Table 1)

Holotype. — Collection CNIGR museum, St Petersburg, 801/11, Novaya Zemlya, Northern Island, Cape Makarov, loc. 801, bed 11, Bashkirian stage, Askynhashskian substage.

Material and occurence. — Bashkirian stage, Askynbashskian substage, Novaya Zemlya, Northern Island, Cape Makarov, loc. 801, bed 11, one colony (collecting of Dr. V. P. Matveev).

Etymology. — From primitive (lat.), very simple.

Description

Small cerioid colony with five to six angles corallites. Intercorallite wall is thin. Major septa thin, long and reach two-third of corallite diameter. Diameter of corallite 4-5 mm, rare 7 mm. Number of major septa 15-18. Minor septa

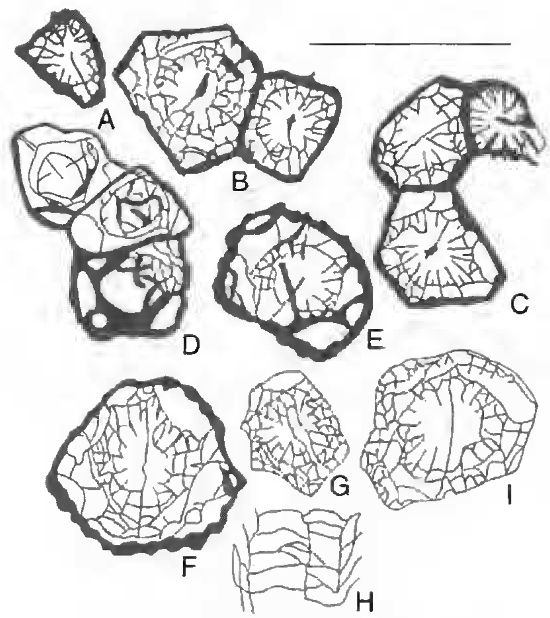

FIG. 7. — *Petalaxis* (*P.*) *stylaxis* group: **A**, **B**, *Petalaxis* (*P.*) *stylaxis* (Trauschold) = *P. stylaxis* var.1, Dobrolyubova, N 17/140 museum PINRAN, Moscow Basin, Moscovian stage, Myachkovian substage; **C**, *Petalaxis* (*P.*) *stylaxis* (Trauschold) = *P. stylaxis* var.2, Dobrolyubova, N 22/140 museum PINRAN, Moscow Basin, Ruza-Ojigova, right bank of Moscow River, down stream from Novaya Ruza, Moscovian stage, Myachkovian substage; **D-F**, *Petalaxis* (*P.*) *stylaxis* (Trautschold), N 32-9-4a/1 CNIGR museum, St Petersburg, Russia, Northern Timan, Sula River section, loc. 32, bed 9, Moscovian stage, Myachkovian substage; **G-I**, *Petalaxis* (*P.*) *primitivum* Kossovaya n.sp., Novlaya Zemlya, Northern Island, Cape Markarov, N 801/1, bed 9, collecting by Dr V. Matveev, Bashkirian stage, Askynbashskian substage. Scale bar: 1 cm.

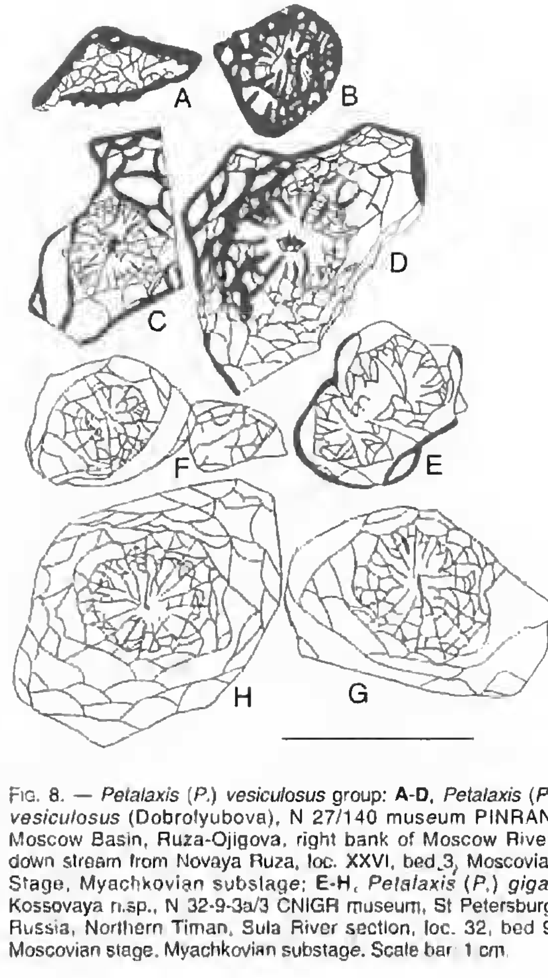

FIG. 8. — *Petalaxis* (*P.*) *vesiculosus* group: **A-D**, *Petalaxis* (*P.*) *vesiculosus* (Dobrolyubova), N 27/140 museum PINRAN, Moscow Basin, Ruza-Ojigova, right bank of Moscow River, down stream from Novaya Ruza, loc. XXVI, bed 3, Moscovian Stage, Myachkovian substage; **E-H**, *Petalaxis* (*P.*) *gigas* Kossovaya n.sp., N 32-9-3a/3 CNIGR museum, St Petersburg, Russia, Northern Timan, Sula River section, loc. 32, bed 9, Moscovian stage, Myachkovian substage. Scale bar: 1 cm.

poorly developed, short and in some corallites they are absent. Thin interrupted column consists of conjoined axial parts of cardinal and counter septa or separated medial plate. Dissepimentarium consists of two or three ranks of interseptal dissepiments and few lonsdaleoid dissepiments. The latter do not form a constant ring. Dissepimentarium is separated from tabularium by thin inner wall. The width of dissepimentarium is 1.0 mm. Tabulae are flat, or slightly concave or convex. Microstructure is of monotrabecular type. Diameter of tabularium 4-4.5 mm. Wdis/Dtab 0.2-0.25.

DISCUSSION

This species differs from *P. stylaxis* by less development of lonsdaleoid dissepiments and more numerous major septa; from *P. kitakamiensis* by rare occurence of lonsdaleoid dissepiments (Fontaine 1991); from *P. penduelensis* by constant and thicker column.

Petalaxis (*P.*) *vesiculosus* group (Figs 8, 9, 10B, C, 13A, B, F, G, 14C-E; Table 2)

SPECIES INCLUDED. — *P.* (*P.*) *vesiculosus* (Dobrolyubova, 1935), *P.* (*P.*) *belinskiensis* Fomichev, 1953, *P.* (*P.*) *lisitschanskensis* Fomichev, 1953, *P.* (*P.*) *gigas* n.sp., *P.* (*P.*) *mohikanus* Fomichev, 1953, *P.* (*P.*) *exilis* Kozyreva, 1974, *P.* (*P.*) *korkhovae* Kozyreva, 1974, *P.* (*P.*) *persubtilis* Kozyreva, 1974, *P.* (*P.*) *confertus* (Kozyreva, 1974), *P.* (*P.*) *mirus* (Kozyreva, 1974), *P.* (*P.*) *evidens* (Kozyreva, 1974).

TABLE 1. — *Petalaxis* (*P.*) *stylaxis* group. **D**, diameter of corallite (mm); **Wdis**, dissepimentarium width (mm); **Dtab**, diameter of tabularium (mm); **S1**, major septa; **S2**, development of minor septa; **DR**, the number of rows of lonsdaleoid dissepiments; **Wdis/Dtab**, the ratio of dissepimentarium width to tabularium diameter; **r**, reduced; **pd**, poorly developed; **d**, developed. The measurements of *P* (*P.*) *stylaxis* are based on Dobrolybova (1935) and Kossovaya's collection and of *P.* (*P.*) *primitivum* is based on the holotype.

	D (mm)	Wdis (mm)	Dtab (mm)	S1	S2	DR	Wdis/Dtab
stylaxis	6-8	1	3-4	13-16	pd	1-2	0.25
primitivum	5	1	4-4.5	17-18	r	2-3	0.2-0.25
kitakamiensis	5-6	1.1	4	16-20	r	1-2	0.27

TABLE 2. — *Petalaxis* (*P.*) *vesiculosus* group (see legend Table 1).

	D (mm)	Wdis (mm)	Dtab (mm)	S1	S2	DR	Wdis/Dtab
vesiculosus	6-12	4.0	3-3.5	10-14	d	2-3	1.3
belinskiensis	7-9	4.0	4.0	17-19	d	2-3	1.0
lisitschanskensis	12-15	7.0	6.0	18-21	d	3	1.2
gigas	11-16	5	5	19-21	d	2-4	1
mohikanus	6-8	2	1	13-18	d	2-4	1.7
exilis	8-9	3	2.5	10-14	r	3-5	1.2
korkhovae	9-15	3.5	2.5	16-18	r	2-4	1.4
persubtilis	9-15	6.0	2.5	15-17	pd	2-4	1
confertus	8-12	2	2	15-17	pd	2-4	1
mirus	7-15	2-3	2	16-18	r	1-2	1-1.5
evidens	13-15	2-2.5	2	19-20	pd	1-2	1-1.7

TABLE 3. — *Petalaxis* (*Grootia*) group (see legend Table 1).

	D (mm)	Wdis (mm)	Dtab (mm)	S1	S2	DR	Wdis/Dtab
ivanovi	6-6.5	0.5	2	13-14	d	0-1	0-0.25
yosti	5-8	2	4.6	18-22	d	0-4	0.4
perapertuensis	5-7	0-1	2.3	17	d	0-1	0-0.4
radians	7-8	–	5	17	d	0	0
santaemariae	5	–	2	19	d	0	0
cantabrica	6-7	0-1	3	23	d	1-2	0.3
wahooensis	5	1.3	3	24	d	1-2	0.4

TABLE 4. — *Petalaxis* (*P.*) *gigas* n.sp. (see legend Table 1).

Sample number	D (mm)	Wdis (mm)	Dtab (mm)	S1	S2	DR	Wdis/Dtab
32-9-4/2	14	3.5	3	20	d	2-3	1
32-9-4/2	14	3	4	21	d	2-3	0.7
32-9-4/2	12.5	3.5	3	20	d	3-4	1.7
20-109a-3/1	11	5	5	19	d	3-4	1
20-109a-3/1	16	5	6	19	d	2-3	0.8

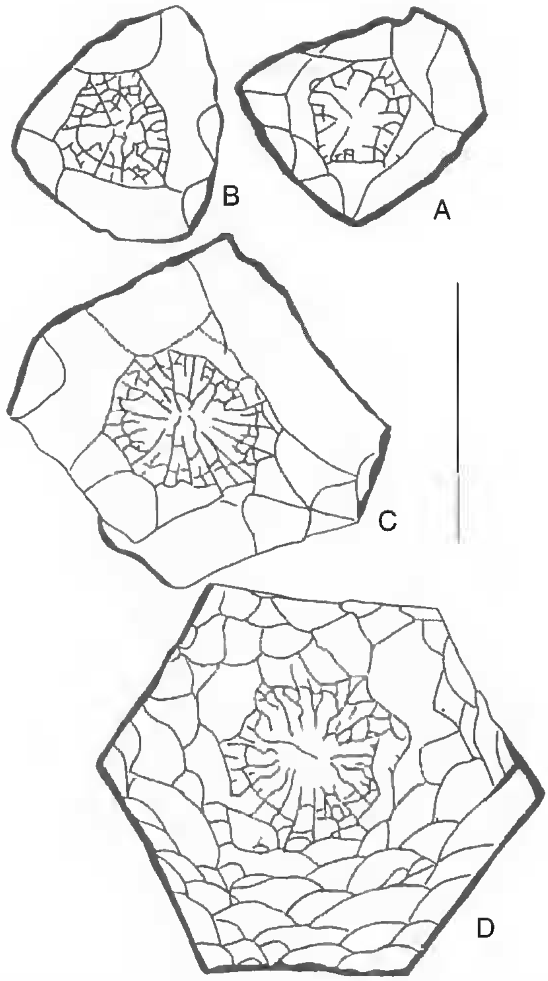

FIG. 9. — *Petalaxis* (*P.*) *vesiculosus* group: **A-D**, *Petalaxis* (*P.*) *gigas* Kossovaya n.sp., N 32-9-4a/2 CNIGR museum, St Petersburg, Russia, Northern Timan, Sula River section, loc. 32, bed 9, Moscovian stage, Myachkovian substage. Scale bar: 1 cm.

DIAGNOSIS. — This group evolved towards the stabilization of minor septa and the widening of the dissepimentarium, which reached a maximum width in Myachkovian time. The most stable features are: (1) a well-developed lonsdaleoid dissepimentarium; (2) the ratio of the dissepimentarium width to the tabularium diameter is equal to one or more. The structure of the axial part is the most changeable feature of representatives of this group. The septal lamellae occur frequently. For species included in *Petalaxis* (*P.*) *vesiculosus* Group, Wdis/Dtab is about 1-1.7. The representatives of this group which are characterized by maximum width of dissepimentarium are most widespread in the middle and upper parts of the Myachkovian substage, where they are srratigraphically important.

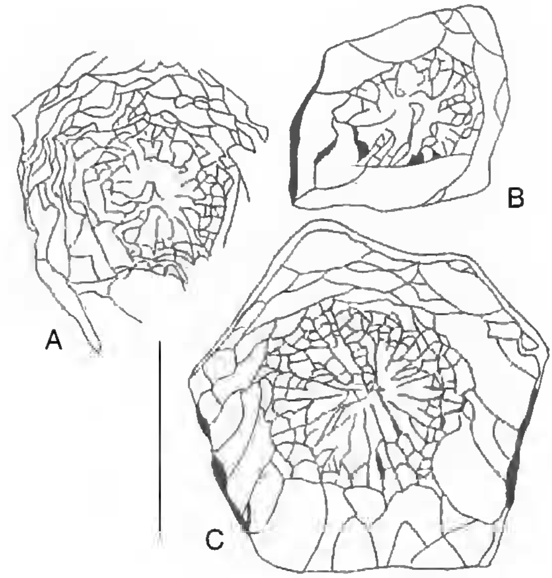

FIG. 10. — **A**, *Petalaxis* (*P.*) *flexuosus* group: *Petalaxis* (*P.*) *orboensis* de Groot, N 32-9-3a/1 CNIGR museum, St Petersburg, Russia, Northern Timan, Sula River section, loc. 32, bed 9, Moscovian stage, Myachkovian substage; **B**, **C**, *Petalaxis* (*P.*) *vesiculosus* group: *Petalaxis* (*P.*) *gigas* Kossovaya n.sp., N 20-109a-3/1 CNIGR museum, St Petersburg, Russia, Northern Timan, Malaya Pokayama section, Volonga River, loc. 20, bed 109a, Moscovian stage, Myachkovian substage, holotype. Scale bar: 1 cm.

Petalaxis (*P.*) *gigas* n.sp.
(Figs 8E-H, 9A-D, 10B, C, 13F, G, 14C, D; Table 3)

HOLOTYPE. — Collection CNIGR museum, St Petersburg, N 20-109a-3/1, Volonga River, Malaya Pokayama section, Sula Formation, Moscovian stage, Myachkovian substage, *Ivanovia* partial range zone, *Petalaxis vesiculosus* species zone.

MATERIAL AND OCCURENCE. — Moscovian stage, Myachkovian substage, Northern Timan, Sula Formation, Myachkovian substage, Volonga River (Malaya Pokayama section), CNIGR museum, St Petersburg, loc. 20, bed 109, two colonies, two transverse and two longitudinal sections Sula River, Sula River section, loc. 32, bed 9.

ETYMOLOGY. — From "gigas" (lat.), enormous.

DESCRIPTION

Cerioid colonies with maximum size 1.0-1.7 m. Corallite 5-6 angle shape. Intercorallite wall thick, sometime waved. Major septa long, nearly

TABLE 5. — *Petalaxis* (*P.*) *flexuosus* group (see legend Table 1).

	D (mm)	Wdis (mm)	Dtab (mm)	S1	S2	DR	Wdis/Dtab
flexuosus	5-7	2	3-4	14-17	d	1	0.6
major	7-9	1.5-2	1.7-2.0	17-22	d	2-3	0.8-1.0
orboensis	6-8	1.7-3.5	3.5-4	17-19	d	1-3	0.5-0.8

TABLE 6. — *Petalaxis* (*P.*) *mcoyanus* group (see legend Table 1).

	D (mm)	Wdis (mm)	Dtab (mm)	S1	S2	DR	Wdis/Dtab
wagneri	4	0-1	2-3.5	14-16	pd	1-2	0.3
mcoyanus	5.4-7.8	0.5-1.0	1.5-1.7	16	pd	1	0.3
donbassicus	5-7	1.0	1.5	14-17	d	1-2	0.6
grootae	4-6	0.7	1.6	14-16	d	1-3	0.4
sexangulus	3-4	1.0	2.5-3	13-15	r	0-1	0.4
intermedius	5-6	1-1.2	2	16-19	r	4	0.6

reach the axis of corallite. Number of major septa-19-21. Minor septum egual à half of major septum. Column thin, constructed from the inner part of the cardinal septum. Cardinal septum short in the poorly distinguished fossula in some corallites. In longitudinal section (Fig. 13G) there are two septal lamellae parallel to the axial lamella of column. Internal wall separates tabularium and dissepimentarium. Tabulae subhorizontal. Dissepimentarium consists of three to four rows of large, convex dissepiments. Microstructure is of monotrabecular type. There are some differences in dimentions of corallites from different localities.

DISCUSSION

New species differs from *P. vesiculosus* by larger diameter of corallites and wider ring of dissepiments.

Petalaxis (*P.*) *flexuosus* group
(Figs 10A, 11, 13E, 14A, B; Table 4)

SPECIES INCLUDED. — *P. flexuosus* (Trautschold, 1879), *P. major* (de Groot, 1963), *P. orboensis* (de Groot, 1963).

DIAGNOSIS. — The nominal species of this group shows a more complex axial structure and a narrow ring of dissepiments. Axial structure consists of the axial lamellae, few irregular radial lamellaes. Peripheral parts of septa can continue into dissepimentarium. The most constant morphological characteristics in corals of this group are a complex axial structure and a narrow dissepimentarium consisting of small dissepiments developed in mature stages. For species included in *Petalaxis* (*P.*) *flexuosus* group Wdis/Dtab is about 0.7-1.

Petalaxis (*P.*) *mcoyanus* group
(Table 5)

SPECIES INCLUDED. — *P.* (*P.*) *wagneri* (de Groot, 1963), *P.* (*P.*) *mcoyanus* (Milne-Edwards *et* Haime, 1852), *P.* (*P.*) *donbassicus* Fomichev, 1953, *P.* (*P.*) *grootae* Sando, 1983, *P.* (*P.*) *sexangulus* (de Groot, 1963), *P.* (*P.*) *intermedius* (de Groot, 1963).

DIAGNOSIS. — This group occupies a position intermediate between the *P. stylaxis* group and *P. flexuosus* group and is characterized by a more complex axial structure, than the former and by a narrower dissepimentarium, than that found in representatives of the *P.* (*P.*) *flexuosus* group. For species included in *Petalaxis* (*P.*) *mcoyanus* group Wdis/Dtab is about 0.3-0.7.

Petalaxis (*Grootia*) group
(Figs 12A, 14F; Table 6)

SPECIES INCLUDED. — *Petalaxis* (*Grootia*) *ivanovi* (Dobrolybova, 1935), *P.* (*G.*) *parapertuensis* (de Groot, 1963), *P.* (*G.*) *radians* (de Groot, 1963), *P.* (*G.*) *santaemariae* (de Groot, 1963), *P.* (*G.*) *cantabricus* (de Groot, 1963), *P.* (*G.*) *wahooensis* Armstrong, 1972, *P.* (*G.*) *yosti* Stevens, 1995.

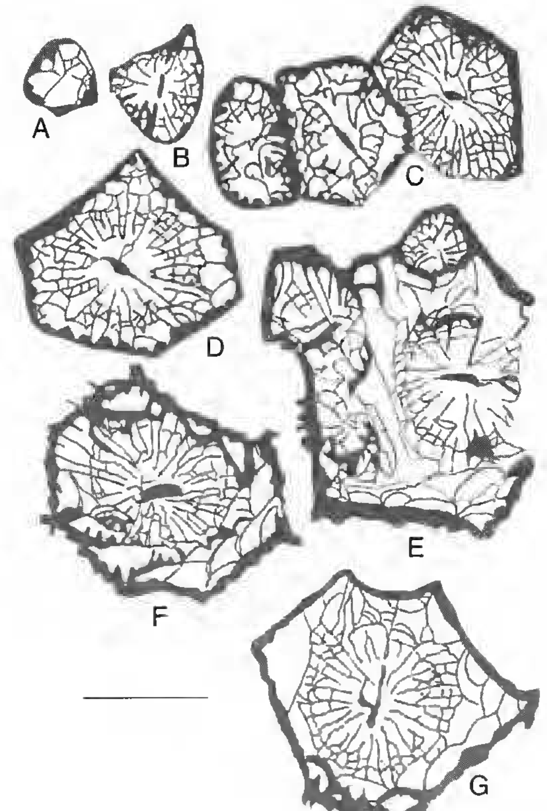

FIG. 11. — *Petalaxis* (*P.*) *flexuosus* group: **A-D**, *Petalaxis* (*P.*) *flexuosus* (Trautschold) N 24/140 museum PINRAN, Moscow Basin, Moscovian stage, Myachkovian substage; **E**, **F**, *Petalaxis* (*P.*) *flexuosus* (Trautschold), N 5-6-1 CNIGR museum, St Petersburg, Russia, Northern Timan, Belaya River section, loc. 5, bed 6, Moscovian stage, Myachkovian substage; **G**, *Petalaxis* (*P.*) *flexuosus* (Trautschold), N 5-5-2 CNIGR museum, St Petersburg, Russia, Northern Timan, Belaya River section, loc. 5, bed 5, Moscovian stage, Myachkovian substage. Scale bar: 0.5 cm.

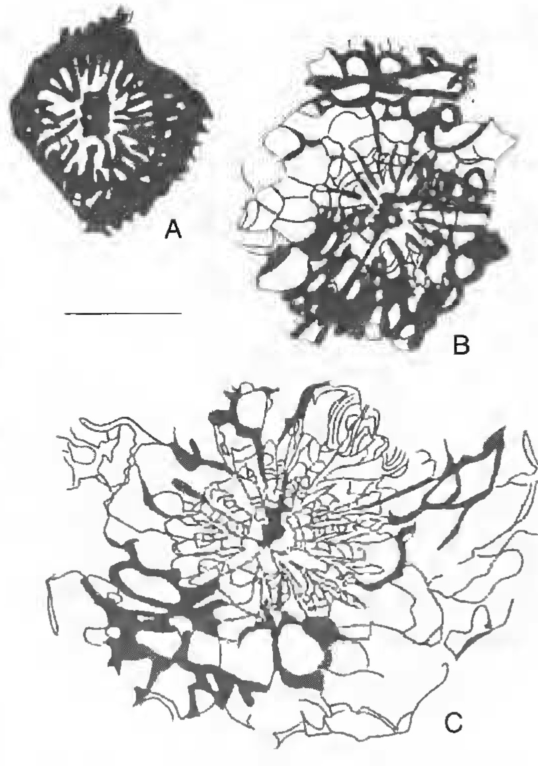

FIG. 12. — *Petalaxis* (*Grootia*) group: **A**, *Petalaxis* (*Grootia*) *ivanovi* (Dobrolyubova), N 88/140 (holotype) museum PINRAN, Moscow Basin, Protopopovo quarries in the vicinity of Kolomna, Moscovian stage, Myachkovian substage; **B**, *Ivanovia* (*Ivanovia*) *podolskiensis* (Dobrolyubova), N 106/140 (holotype), museum PINRAN Moscow Basin, Schurovo, Moscovian stage, Myachkovian substage; **C**, *Donastraea bella* (Dobrolyubova) N 68/140 (holotype) museum PINRAN, Moscow Basin, Podolsk, Moscovian stage, Myachkovian substage. Scale bar: 0,5 cm.

DIAGNOSIS. — This group embraces species characterized by the absence or weak development of lonsdaleoid dissepiments and had been primerally determined as *Hillia* n.g. by de Groot (1963). This name was preoccupied (see Sando 1983). Sando considered this group as a special group within the *Petalaxis* genus. The genus was renamed as *Grootia* by Yu (1977). Most of the species of this group are known from the Bashkirian and Moscovian deposits of the Cantabrian Mountains (de Groot 1964). Only one species [*P.* (*Grootia*) *ivanovi*] from the Moscow Basin can be included and it is characterized by an absent or very weak development of a lonsdaleoid dissepimentarium. Species included in *Petalaxis* (*Grootia*) group are characterized by Wdis/Dtab 0-0.4

Genus *Cystolonsdaleia* Fomichev, 1953

DIAGNOSIS. — As *in* Fomichev (1953) and Hill (1981). Astreoid colonies of Petalaxidae family. The main morphological features that have been used as a basis for taxonomical revision of the astreoid colonies of Petalaxidae are: the type of colony, the differences in the axial structure of corallites and the development of minor septa.

Genus *Ivanovia* Dobrolyubova, 1935

Ivanovia Dobrolyubova, 1935: 35. – Hill 1981: F403 (partly). – Fomichev 1953: 477. – Wu & Lin 1992: 105, 106.

Cystophora – Dobrolyubova 1935: 20. – Fomichev 1953: 407.

Subgenus *Ivanovia* (*Ivanovia*) (Dobrolyubova, 1935) (Figs 12B, 15C, D, 16C, D)

TYPE SPECIES. — *Ivanovia podolskiensis* Dobrolyubova, 1935 (Figs 12B, 16C, D). Holotype: sample 106/140 Museum of Palaeontological Institute of Russian Academy of Science, Moscow (Dobrolyubova 1935: 35-36, plate XII, figs 1-2).

AGE AND LOCALITIES. — Moscovian stage, Podolskian and Myachkovian substages of Moscow Basin, Donets Basin, Kashirian? Podolskian substages of Spain. Moscovian stage of China.

SPECIED INCLUDED. — *I.* (*I.*) *podolskiensis* Dobrolyubova, 1935, *I.* (*I.*) *freieslebeni* (Fischer, 1830), *I.* (*I.*) *expansa* Dobrolyubova, 1935, *I.* (*I.*) *sparsa* (Fomichev, 1953), *I.* (*I.*) *cystiseptata* (Fomichev, 1953), *I.* (*I.*) *nadeini* (Fomichev, 1953), *I.* (*I.*) *aster* Fomichev, 1953, *I.* (*I.*) *? pogrebitskyi* Fomichev, 1953, *I.* (*I.*) *occidentalis* Fomichev, 1953) (= *Polythecalis occidentalis* Fomichev, 1953), *I.* (*I.*) *intermedia* Wu *et* Lin, 1992, *I.* (*I.*) *mirabilis* Wu *et* Lin, 1992.

DIAGNOSIS. — Aphroid colony with some traces of walls; major septa long, but few reaching columella, dilated in tabularium; minor septa present or not; septa discontinious in dissepimentarium; axial structure compact, consists of thickned part of the counter septum or thickened median plate; sometime axial structure is very simple: periaxial tabellae slightly inclined. Septal microsrructure of monotrabecular type (Fig. 15E, F).

Subgenus *Ivanovia* (*Protoivanovia*) X. Yu, 1977

TYPE SPECIES. — *Protoivanovia regularis* X. Yu, 1977.

SPECIES INCLUDED. — *Ivanovia* (*Protoivanovia*) *regularis* X. Yu 1977, *I.* (*P.*) *ditulathecata* Wu *et* Lin, 1992, *I.* (*P.*) *mayicunensis* Wu *et* Lin, 1992, *I.* (*P.*) *shanchengziensis* Wu *et* Lin, 1992, *I.* (*P.*) *shanchengziensis pluriseptata* Wu *et* Lin, 1992.

Ivanovia (*Procystophora*) Kossovaya n.sg. (Fig. 16E, F)

TYPE SPECIES. — *Cystophora densivesiculosa* Dobrolyubova 1935, plate VII, figs 3-4. Holotype: collection of the Museum of Palaeontological Institute of Russian Academy of Science, Moscow, N140, thin sections 188-190.

SPECIES INCLUDED. — *Ivanovia* (*Procystophora*) *densivesiculosa* (Dobrolyubova, 1935) [= *Cystophora densivesiculosa* Dobrolyubova, 1935] (Fig. 16E, F), *I.* (*P.*) sp. 1 [= *I. freieslebeni* (Stuckenberg, 1888) *in* Dobrolyubova 1935, plate IV, figs 1, 2)

AGE AND LOCALITIES. — Middle Carboniferous, Moscovian stage, Myachkovian substage, right bank of Moscow River, near Sonino village.

DIAGNOSIS. — Cerioid-thamnasterioid colonies with or without traces of walls: major septa rather long, minor septa of inconstant lenght present; axial structure compact, comprising thickened median plate and sometimes few short lamellae with few axial tabellae arranged in cones; periaxial tabulae sagging, some peripheral clinotabellae. Microstructure of septa-multitrabecular.

Donastraea n.g. (Figs 15F, 16G, H, 12C)

Lonsdaleiastraea Fomichev, 1953: 498 (partly).

Cystophora – Dobrolyubova 1935: 27 (partly).

TYPE SPECIES. — *Lonsdaleiastraea cystiseptata* Fomichev, 1953. Holotype: CNIGR museum, coll. 122/5030, (Fomichev 1953, plate XLI, fig. 2) (Fig. 16G, H).

SPECIES INCLUDED. — *Donastraea cystiseptata* (Fomichev, 1953) [=*Lonsdaleiastraea cystiseptata* Fomichev, 1953] (Fig. 16G, H), *D. yakovlevi* (Fomichev, 1953) [=*Polythecalis yakovlevi* Fomichev, 1953], *D. bella* (Dobrolyubova ,1935) [=*Cystophora bella* Dobrolyubova, 1935] (Fig. 15F).

AGE AND LOCALITY. — Moscovian stage, Myachkovian substage-the base of the Kasimovian? stage, Donets Basin, limestone O1, to the east from Rjazantsev village.

ETYMOLOGY. — Derivation of name from Don River.

DIAGNOSIS. — Aphroid colonies with axial structure from simple median plate to compound structure of regular shape with numerous radial lamella, sometime forming the structure cone-in-cone, inner series of tabellae sagging. Dissepimentarium wide, consisting of the horizontal rows of dissepiments. Naotic dissepiments and septal carinae may be presenr. Microstructure of multitrabecular type.

Genus *Benxiphyllum* Wu *et* Lin, 1992.

Cystophora Yabe *et* Hayasaka, 1916: 76. – Yabe & Sugiyama 1944: 74, pl. 3, figs 1-4.

TYPE SPECIES. — *Cystophora manchurica* Yabe *et* Hayasaka, 1916: 70; Yabe & Sugiyama 1944: 74, pl. 3, figs 1-3.

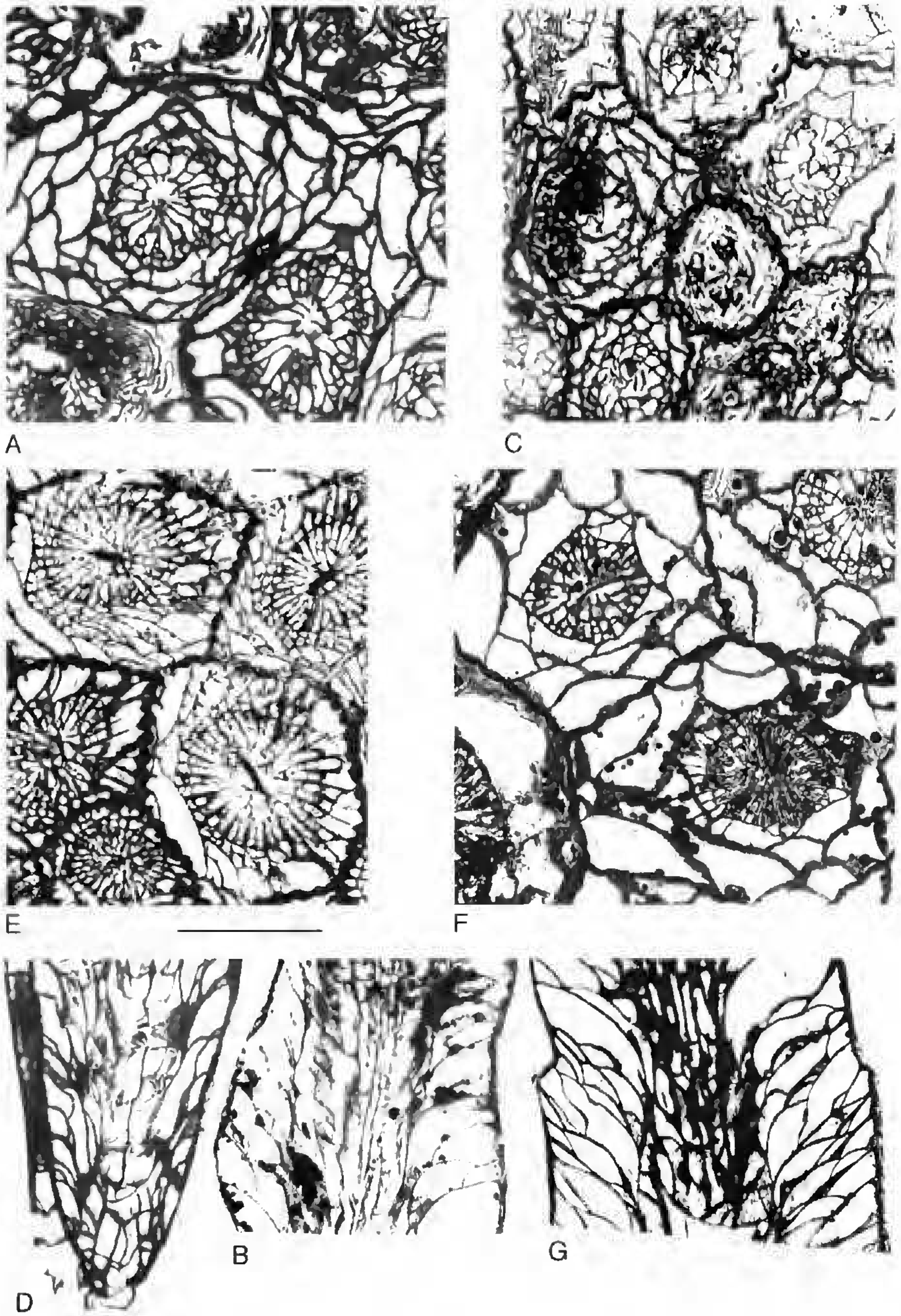

FIG. 13. — **A**, **B**, *Petalaxis* (*P.*) *vesiculosus* (Dobrolyubova), N 32-9-3a/3 CNIGR museum, Northern Timan, Sula River section. loc. 32, bed 9, Sula Formation, Myachkovian substage, (A) transverse section, (B) longitudinal section; **C**, **D**, *Petalaxis* (*P.*) *stylaxis* (Trautschold), N 32 -9-4a/1 CNIGR museum, Northern Timan, Sula River section. loc. 32 , bed 9, Sula Formation, Myachkovian substage, (C) transverse section, (D) longitudinal section; **E**, *Petalaxis* (*P.*) *flexuosus* (Trautschold), N 5-6-1 CNIGR museum, Northern Timan, Belaya River section, loc. 5 , bed 9, Sula Formation, Myachkovian substage; **F**, **G**, *Petalaxis* (*P.*) *gigas* Kossovaya n.sp., N 32-9-4a/2, Northern Timan, Sula River section. loc. 32 , bed 9, Sula Formation, Myachkovian substage, (F) transverse section, (G) longitudinal section. Scale bar: 0.5 cm.

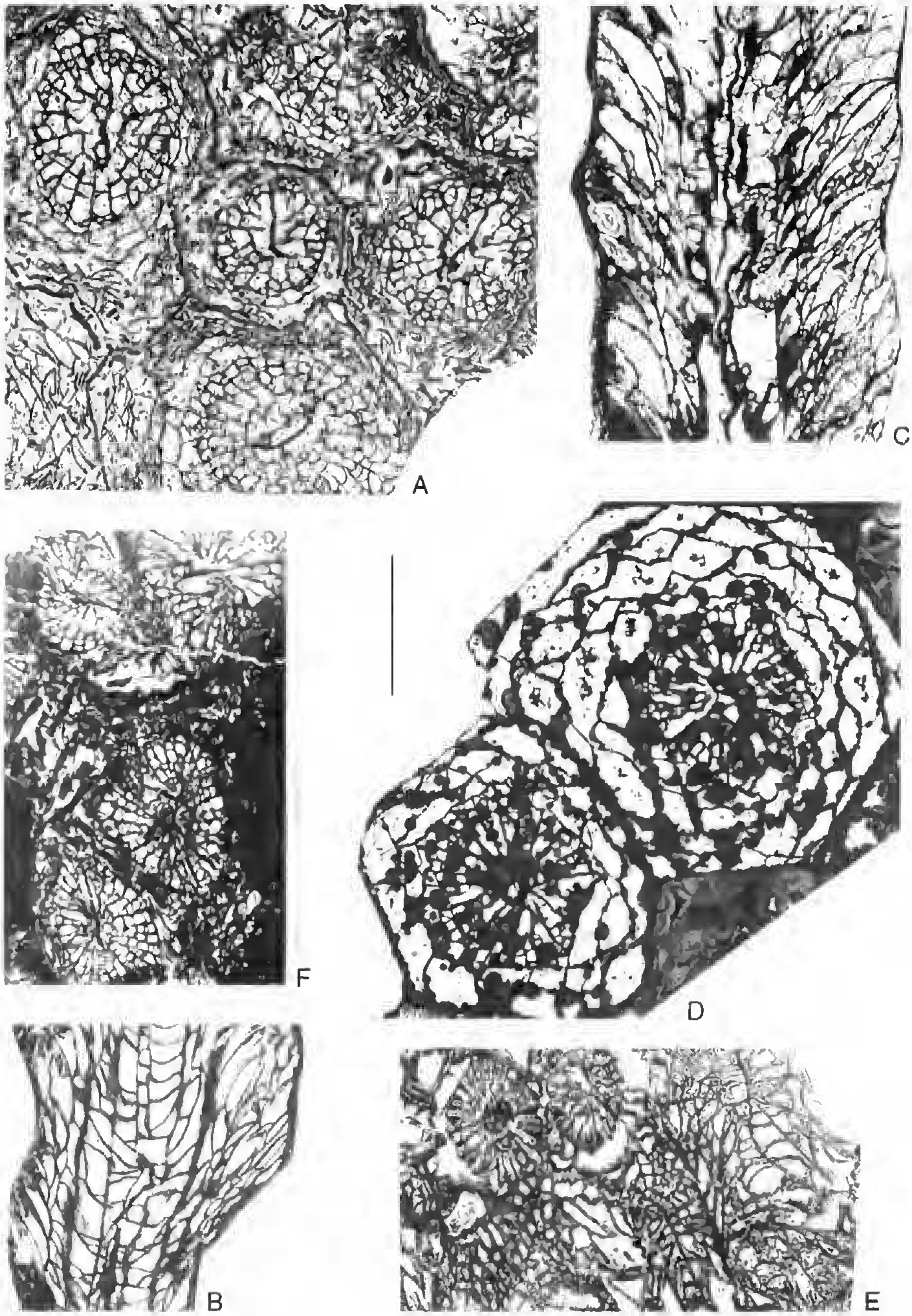

FIG. 14. — **A**, **B**, *Petalaxis* (*P.*) *orboensis* (de Groot), N 32-7-3/1 CNIGR museum, Northern Timan, Sula River section, loc. 32, bed 7, Sula Formation, Myachkovian substage, (A) transverse section, (B) longitudinal section; **C**, **D**, *Petalaxis* (*P.*) *gigas* Kossovaya n.sp., N 20-109a-3/1 CNIGR museum, Northern Timan, Malaya Pokayama section, loc. 20, bed 109, Sula Formation, Myachkovian substage, (C) transverse section, (D) longitudinal section; **E**, *Petalaxis* (*P.*) *persubtilis* Kozyreva, N 31-9-1/4 CNIGR museum, Northern Timan, Sula River section, loc. 31, bed 9, Askynbashskian substage; **F**, *Petalaxis* (*P.*) *intermedius* (de Groot), N 32-7-3/3, Northern Timan, Sula River section, loc. 32, bed 9, Sula Formation, Myachkovian substage. Scale bar: 0.5 cm.

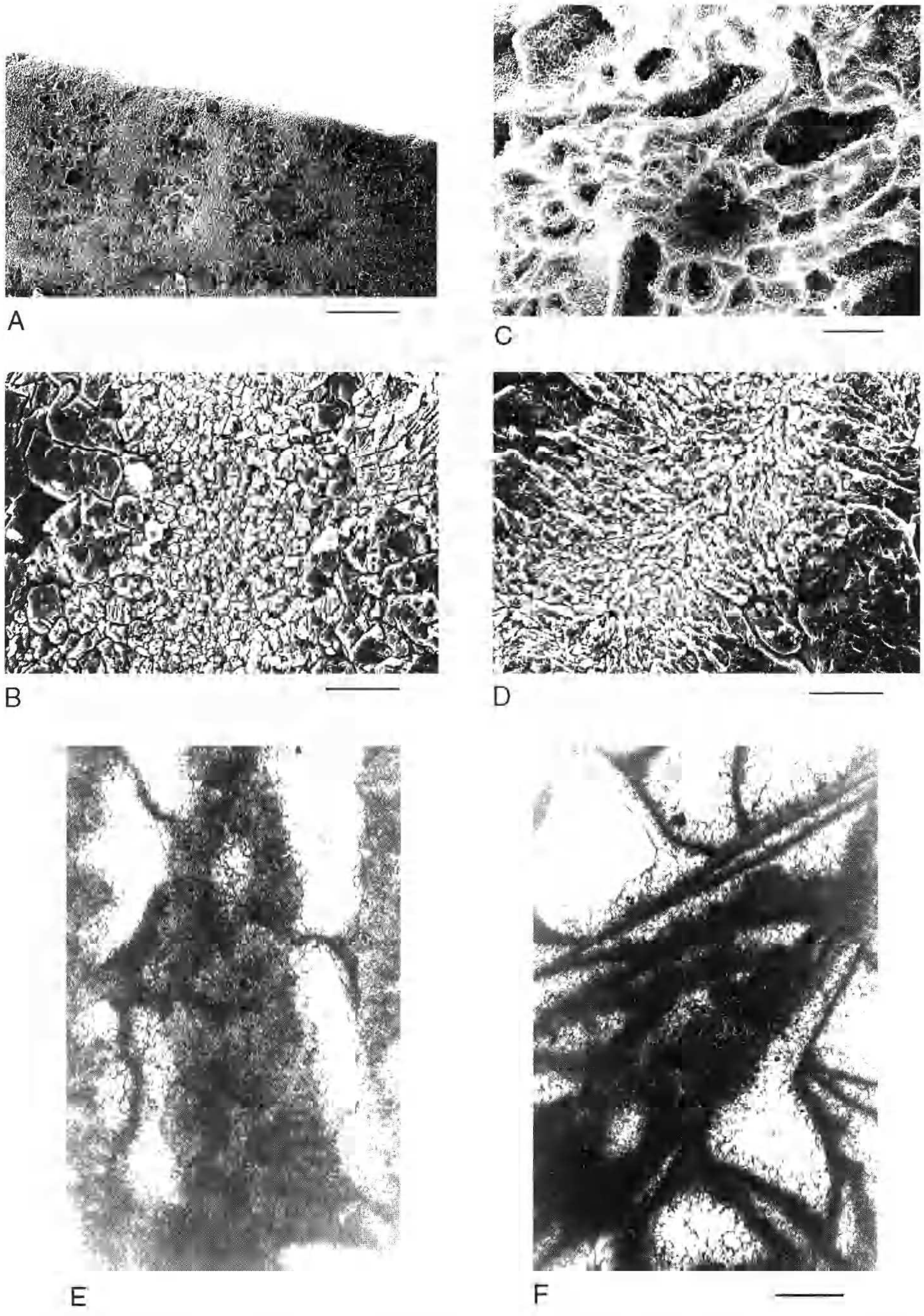

FIG. 15. — **A**, **B**, *Petalaxis* (*P.*) *stylaxis* (Trautschold), N 32-9-4a/1, Northern Timan, Sula River section, loc. 32, bed 9, Sula Formation, Myachkovian substage, (A) transverse section of corallite, (B) transverse section of septum (SEM); **C**, **D**, *Ivanovia podolskiensis* Dobrolyubova, P-15-1a CNIGR museum, Moscow region, Podolsk quarry, bed 15, Podolskian substage, (C) transverse section of corallite, (D) transverse section of septum; **E**, *Cystophorastraea moelli* (Stuckenberg), N 10/140 museum PINRAN, Moscow, Moscow Basin, Myachkovian substage; **F**, *Procystophora bella* (Dobrolybova), N 140 museum PINRAN, Moscow Basin, Myachkovian substage. Scale bars: A, 200 µm; B, D, 20 µm; C, 600 µm; E, F, 140 µm.

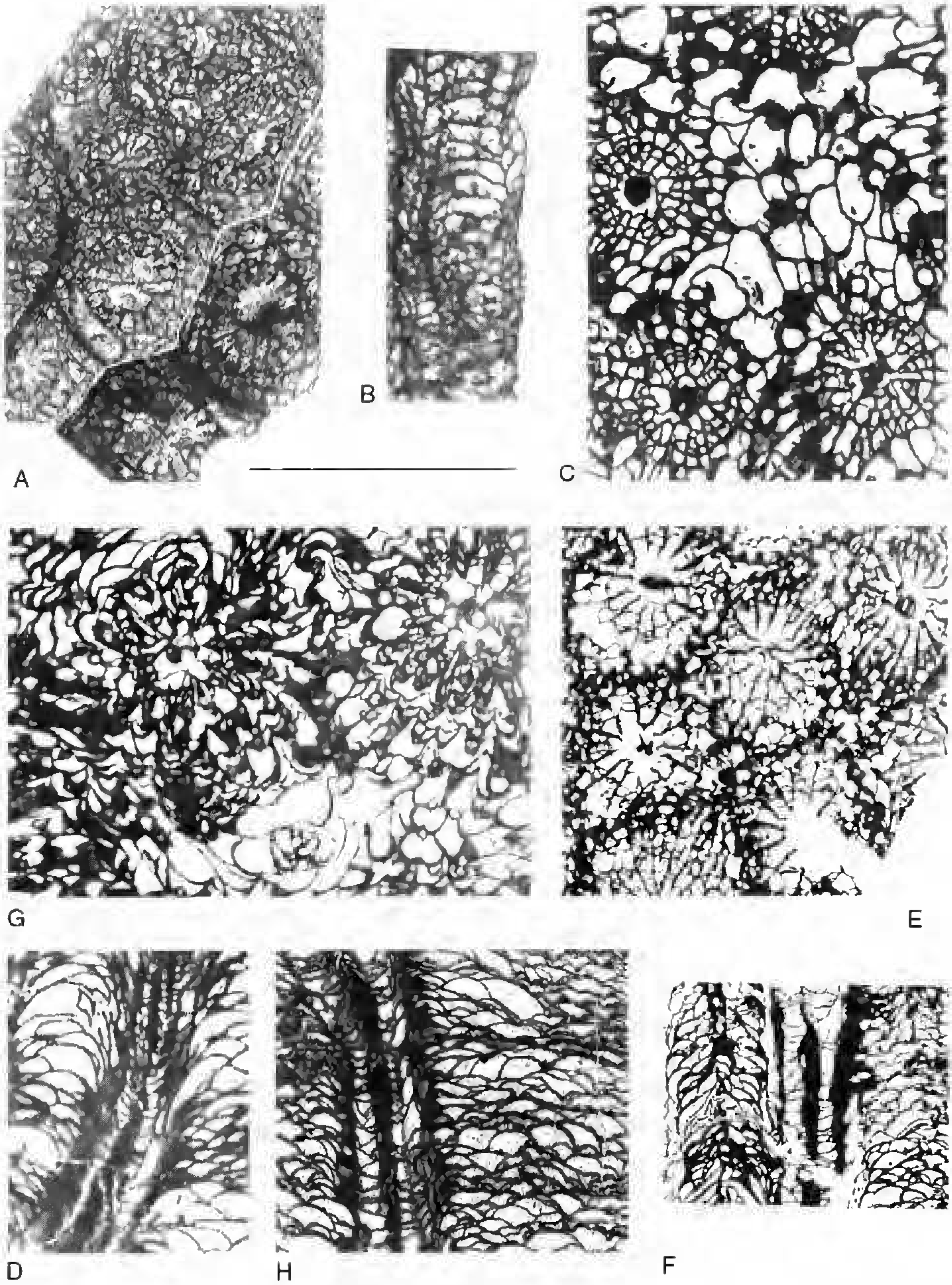

FIG. 16. — **A**, **B**, *Petalaxis* (*P.*) *primitivum* Kossovaya n.sp. CNIGR museum, St Petersburg, N 801-11, Novaya Zemlya, Northern Island, Makarov Cape, loc. 801, bed 11, Bashkirian stage, Askynbashskian substage (collecting of Dr V. P. Matveev), (A) transverse section, (B) longitudinal section; **C**, **D**, *Ivanovia* (*Ivanovia*) *podolskiensis* Dobrolyubova PINRAN, coll. 140, N 106/140, Moscow Basin, Myachkovian substage, Schurovo village, (C) transverse section, (D) longitudinal section; **E**, **F**, *Ivanovia* (*Procystophora*) *densivesiculosa* (Dobrolyubova), PINRAN (Dobrolyubova, 1935), coll. 140, N 65/140, holotype, Moscow Basin, Myachkovian substage, near Sonino village, (E) transverse section, (F) longitudinal section; **G**, **H**, *Donastraea cystiseptata* (Fomichev), CNIGR museum (Fomichev 1953), coll. 5030, holotype N 436/503. Donets Basin, limestone O1, to east from Rjazantsev village, (G) transverse section, (H) longitudinal section. Scale bar: 1 cm.

SPECIES INCLUDED. — *Benxiphyllum manchurica* (Yabe *et* Hayasaka, 1916); *B. bacilliforme* Wu *et* Lin, 1992; *B. temcolumnarum* Wu *et* Lin. 1992; *B. brachyseptatum* Wu *et* Lin, 1992; *B. ellipticum* Wu *et* Lin, 1992.

AGE. — The upper part of the Late Carboniferous (Moscovian stage).

DIAGNOSIS. — Corallum compound, cystose-aphroid, wall occasionally appeared. Septa of two order, distinctly thickened, with large almond-shape columella (Amygdalophylloid) in transverse section, in which there is a texture of middle and radial lines. Tabulae inclined towards the inner, lateral tabellae developed.

PHYLOGENY

Evolution of Petalaxidae could be subdivided into main phases within the uppermost lower Bashkirian to the end of the Moscovian. The appearance of the first representatives of *Petalaxis* seems to be the result of colonization of numerous niches in stabilized environments. The stepwise increase in diversity was interrupted by the unfavorable conditions at the end of Bashkirian in which only a few species survived in the basins.

The beginning of the radiation phase of Petalaxidae family coinsides with the maximum diversity level of the other groups of rugose corals (Kossovaya 1996). The structural changes of massive Petalaxidae have resulted in the increase in the degree of integration (Fig. 6). Microstructural changes are displaied by gradual change in the type of microstructure, from monotrabecular (typical for most species of *Petalaxis*) to inconstant multitrabecular [characteristic for *Donastraea* (Figs 11C, 15F)] and gradual stabilization of the multitrabecular structure in *Donastraea*.

Phyletic evolution has resulted in the following skeletal expression in *Petalaxis-Ivanovia* (*Ivanovia*) lineage: (1) simplification of the inner structure of the earliest species with locally interrupted wall; (2) increase in the width of the dissepimentarium as a connecting structure between corallites.

The gradual change is characteristical for change in the type of colony from cerioid-aphroid to thamnasterioid in the *Ivanovia* (*Ivanovia*)-*Ivanovia* (*Procystophora*) lineage. The completness of inner structure and stabilization of multitrabecular structure seems to be the main evolution tendency in the *Ivanovia* (*Ivanovia*)-*Donastraea* lineage.

CONCLUSIONS

The evolution history of Petalaxidae from the origination of cerioid *Petalaxis stylaxis* with simple inner structures (Fig. 6), followed by rather rapid expansion and morphological diversification both in *Petalaxis* and related groups resulting in morphological innovation, could be subdivided into two phases.

The first phase, recovery of long duration, is characterized by stabilization of several *Petalaxis* lineages, shown here as morphogenetic groups. Stabilization of minor septa occured within different groups of *Petalaxis* after a short period of ecological depression at the beginning of the Moscovian. Then, the flourish of Petalaxidae was established within the Podolskian-Myachkovian interval (Fig. 6). The second phase of adaptive radiation with increase both in the generic and specific diversity is characterized by morphological innovation expressed in the increase in degree of the integration in colonies. After the origination of aphroid *Ivanovia* (*Ivanovia*) with simple axial structure a few trends are displaied with the appearance of thamnasterioid type of colony *Ivanovia* (*Procystophora*) n.sg. and aphroid colonies with gradually complicated axial structures (*Donastraea* n.g.).

The paleogeographical realm of the *Petalaxis* species are very wide; it embraces all the margin shelf of Tethyan paleoocean, including both the Peri-tethyan basins surrounding the Euroamerican paleocontinent and numerous epicontinental basin of eastern part of Tethyan. Species of *Ivanovia* lineage have a more narrow realm. They were widespread both in eastern and southern margin shelf basins of Euroamerican palaeocontinent and east-northern margin basins of Tethyan ocean. At the same time representatives with most complete axial structure of *Donastraea* and *Benxiphyllum* lineages occur in the southern margin basins of Angarian and Euroamerican paleocontinents.

It seems possible to consider *Lytvophyllum* Dobrolyubova, 1941 as an ancestor of the Petalaxidae because of the similarity of the budding of the earliest *Petalaxis* (*P. stylaxis* group). Mature stages of fasciculate *Lytvophyllum* species characterized by very high variability are widespread in the recovery assemblage after the Mid-Carboniferous event (Kossovaya 1996).

ADDENDUM. — After the drawing up of this article, an important work on Petalaxidae family was published by Bamber & Fedorowski (1998). Unfortunatly, the material from that publication are not taken in account in the present paper.

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